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Abstract

Low elevation ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.) forests of the northern Rocky Mountains historically experienced frequent, low intensity fires that maintained open, uneven-aged stands. A century of fire exclusion has led to denser ponderosa pine forests with higher competition for resources, higher tree stress, and greater risk of insect attack and stand destroying fire. Active management intended to restore historic stand conditions includes selective thinning and prescribed fire application. However, little is known about the differential effects of these management practices on the physiological performance, defense and reproductive output of ponderosa pine. We examined the physiological performance, resin flow and reproductive output of second growth ponderosa pine trees at the Lick Creek Experimental Site in the Bitterroot National Forest, Montana nine years after the application of four treatments: thinning, thinning followed by spring (wet) prescribed fire, thinning followed by fall (dry) prescribed fire, and unthinned control stands. We asked whether active management improves physiology, defense and reproduction of ponderosa pine and whether these functions are sensitive to the specific active management treatment. Results corroborate our previous finding that active management of second growth ponderosa pines by either thinning or thinning followed by prescribed burning improves tree water status. We also found that cone production is significantly higher in trees from actively managed stands. However, resin flow did not vary across treatments (including control). Field and greenhouse observations suggest that some reproductive traits vary depending on the specific active management treatment. Overall, trees subjected to thinning followed by either spring or fall burning produced cones with higher number of total and filled seeds

relative to trees in control and thin-only treatments. We also found that cones of trees subjected to thinning followed by spring burning produced significantly smaller seeds (lower mass) relative to all other treatments. Consistent with our field results, greenhouse studies revealed that filled seeds from the spring burn treatment exhibited significantly lower germination rates relative to all other treatments and tended to produce smaller seedlings. In contrast, trees subjected to fall burn tended to exhibit similar or slightly higher reproductive output relative to all other treatments and the resulting seeds produced seedlings with slightly higher biomass. These results suggest that the specific management treatment may have implications on reproductive output traits and long-term recruitment of second growth ponderosa pine. To our knowledge this is the first time where management-induced differences in reproductive output have been documented for ponderosa pine. If corroborated by further studies, our results have important implications for ecological restoration.

Introduction

Fire exclusion during the past century has caused dramatic changes in the structure and function of ponderosa pine forests of the northern Rocky Mountains. Because of the negative effects of fire exclusion, prescribed fire and forest thinning are increasingly used to restore historic stand structure, reduce the risk of catastrophic fire, and improve forest productivity (Arno et al. 1995, Powers and Reynolds 2000). Little is known about the differential physiological and functional responses of ponderosa pine to thinning and prescribed fire treatments.

Historically, ponderosa pine forests dominated much of the northern Rocky Mountains forming open stands maintained by low intensity surface fires that burned every 5-25 years (Arno 1988, Martin 1982). Euro-American settlement of the west was followed by a decrease in the fire frequency in much of the ponderosa pine forest systems. As a consequence, ponderosa pine forests have dramatically changed in the past century (Covington and Moore 1994). Most ponderosa pine forests in the northern Rocky Mountains are second growth stands with high tree density relative to historic conditions (Hartwell et al. 2000). The denser stands resulting from fire exclusion display greater competition for resources and greater risk of pathogen outbreaks, insect attack, and stand-replacing fires (Feeney et al., 1998). This suggests that partial restoration of historic conditions may be realized by removing competing trees through active management.

Thinning, which is used to restore historic structural conditions, is often followed by prescribed fire, which is used to reduce fuel. Numerous studies have examined the effects of thinning and prescribed fire on tree growth, nutrient cycles, mortality, and

recruitment in ponderosa pine systems (Monleon et al. 1997, Arno et al. 1996). Historically, ponderosa pine forests of the northern Rocky Mountains burned during the late summer and early fall (Agee, 1993). However, much prescribed burning in the northern Rocky Mountains is conducted during spring months when conditions are cooler and moister, to reduce burn severity, and to support better smoke dispersal. The response of ponderosa pine to prescribed fire may be sensitive to the season in which burning is implemented.

Results from our research in 2001 at the Lick Creek demonstration site suggest that decreases of basal area either by thinning or thinning followed by burning (spring and fall) ameliorated physiological performance of second growth ponderosa pine. We found greater photosynthesis rates and stomatal conductance under similar environmental conditions in all active management treatments relative to the control. Reductions of basal area due to treatments also resulted in higher needle water potential early in the morning in all treatments relative to the control, indicating higher water availability. Soil relative water content (% volume) up to 45 cm below the soil surface did not differ among treatments, including control. While active management by either thinning or thinning followed by prescribed fire ameliorated tree performance, our results suggested that the specific treatments did not have major influences on the long-term tree performance. We concluded that, in light of other benefits of fire to ponderosa pine systems, fire may be applied in the fall or spring after stand thinning, under the specific conditions used, without degrading long-term ponderosa pine health or productivity (Peters 2002).

While this provides valuable baseline information, additional information is required before concluding that fire has no additional benefit or negative effect on ponderosa pine physiological performance and growth relative to thinning alone. For example, while results from 2001 suggest an increased potential for carbon acquisition via photosynthesis in treated plots (whether thinning alone or thinning followed by spring or fall burning), it is not known whether this additional carbon available to trees is allocated to similar functions (e.g. reproduction or defenses against herbivores) in thinned or thinned and burned stands. While 9 years after treatment, measures of soil and needle nutrient content did not reveal differences between the thin and burn treatments, low intensity fire is thought to initially (within the first year) ameliorate nutrient cycling in ponderosa pine systems (Covington and Sackett 1992; Kaye and Hart 1998). Pulses of available nutrients immediately after treatment in burned plots may preferentially shift resource allocation towards nutrient-demanding functions such as defense and reproduction or may increase the quality of these functions (Cregg 1994). Seed production, seed quality, and resistance to insect attack have direct implications for ecosystem-scale health and knowledge of potential differences due to management would be of great value in making forest management decisions.

Our research objectives were twofold. Firstly, we conducted follow up research to the 2001 field season to corroborate patterns in photosynthesis, water potential, and soil moisture. Because results from summer 2001 showed that foliage from treated plots tended to have a higher proportion of younger needles relative to control plots, and older pine needles tend to have lower rates of photosynthesis (see also Clark et al. 1995), we also explored whether age-related reductions of needle photosynthesis rates varied

between treatments. Such measurements allowed us to better assess overall differences in carbon acquisition between treatments. We measured predawn water potential in 2002 to corroborate patterns from daytime water potential measured in 2001; predawn water potential better reflects tree water status because it represents water potential at, or near, equilibrium with the environment. The second goal of our research was to examine whether additional carbon acquired by ponderosa pine in response to basal area reductions (relative to control plots) is equally allocated to reproduction and defense in thinned and thinned plus burned units. We examined potential mid-term (9-10 years after treatment) effects of fire, relative to thinning alone, and of burning season on ponderosa pine resin flow and reproductive output in western Montana.

Carbon-based oleoresin stored within the resin ducts of xylem is the most important defense against insect attack of pine trees (Berryman, 1972). Higher resin volume is associated with greater resistance to *Dendroctonus* pine beetles (Smith 1975) because resin creates a physical barrier to beetle invasion. The degree of resistance can be quantified in the field by inflicting a wound penetrating to the xylem and measuring the subsequent volume of resin flow. Increased resin flow rate may be, to some degree, inducible (Raffa and Berryman 1982). In ponderosa pine, Kolb et al. (1998) found higher resin flow in managed stands with lower tree densities than unmanaged stands, and prescribed fire has been shown to increase resin flow in the short term (Feeney et al. 1998). Furthermore, improved tree physiological health can be associated with increased resin flow (Kolb et al. 1998), which is important in light of increased physiological activity found at our Lick Creek site in 2001 (Peters 2002).

Natural regeneration can be influenced differently by different forest management practices (Shearer and Schmidt 1999, Bailey and Covington 2002). More open canopies can increase the intensity of competition on seedlings by increasing herbaceous cover (Moore and Dieter 1992). Prescribed fire can kill many ponderosa pine seedlings and saplings (Harrignton and Sackett 1990), but can improve seedling establishment by exposing mineral soil and increasing soil moisture content near the soil surface (Haase 1986). While different management choices have important environmental effects on the natural regeneration of ponderosa pine, seed supply, and thus tree reproductive output, can also strongly affect regeneration (Schubert 1974) and may be influenced by thinning and/or burning. Basal area reduction can increase cone production of individual pines (Karlsson 2000). In the short term, wildfire can reduce reproductive output in severely scorched trees (Rietveld 1976). Higher physiological activity of pines in actively managed units relative to controls, as measured at Lick Creek in 2001 (Peters 2002) may provide greater carbon resources in managed trees, enabling greater reproductive output. In addition to seed quantity output, possible treatment-induced differences in seed germination and seedling growth would provide valuable insight into tree resource allocation as well as treatment related regeneration potential.

Cone crops in ponderosa pine vary substantially from year to year, with years of abundant seed production ('mast years') followed by years of medium to low seed production. Such cyclic reproductive strategy appears to reduce seed destruction by various predators (Silvertown 1980) but the environmental and physiological factors that control this periodicity are poorly understood. We were fortunate in this project to have a highly productive mast year for cone harvest in autumn 2002.

Consistent with our 2001 research at Lick Creek, the underlying general question was: Does ponderosa pine benefit from prescribed fire relative to thinning alone? Our 2002 research explored the more specific question: Does mid-term ponderosa pine allocation to reproduction and defense differ between the four management options of thinning, thinning followed by prescribed spring fire, thinning followed by prescribed fall fire, and untreated controls?

Methods

Study Site

The study area is located in the Lick Creek Experimental Site in the Bitterroot National Forest of western Montana, latitude 46°5' N, longitude 114°15' W. The site is dry, with approximately 500mm of average annual precipitation, about half of which falls as snow (Gruell et al. 1982). The stand used in this study occupies a moderately steep, south-facing slope near 1500m of elevation that has been actively managed for about 90 years. The site was dominated by pole-sized ponderosa pines about 70 years of age that arose after selective cutting. A small portion of the remaining trees were Douglas-fir (*Pseudostuga menziesii*). The original stand of old ponderosa pine was selectively harvested around 1909 and again in the 1950's. The stand was pre-commercially thinned in the 1960's and slash was left untreated. Trees responded rapidly to this treatment with substantial increases in diameter growth (Arno 1999).

In 1991, twelve study units approximately 3-4 hectares each were established adjacent to each other in a research design of four treatments with three replicates. Nine thinned units received a stand density reduction treatment and three units located

immediately upslope were left unthinned to serve as controls. Three of the nine thinned units received one of the three prescribed fire treatments, selected randomly: spring burn, fall burn, or no burn. In this paper, we use the term "treated unit" to distinguish the thinned units from the untreated control units. The following terminology is used in this paper to designate the three treated unit types: thinning only = thin-only; thinning followed by wet, spring prescribed fire = spring-burn; thinning followed by dry, fall prescribed fire = fall-burn. Twelve 0.04 hectare circular plots were laid out systematically, 33m apart within each of the 12 units. Sampling of stand characteristics, soil resource availability, and tree response took place in these plots in summer 2001, with some additional data collected in summer, 2002.

The application of treatments was initiated in 1992, when all nine thinning units were commercially thinned to substantially reduce Douglas-fir of all sizes and remove smaller ponderosa pine with the objectives of reducing competition for remaining pines and reducing the potential for crown fire (Harrington 1999a). Only merchantable trees were removed, leaving some of the slash on the site. Basal area was reduced from a preharvest average of approximately 21m^2/ha, 93% of which was ponderosa pine, to approximately 14m^2/ha, 98% of which was ponderosa pine. Stand density was reduced from 420 trees/ha to 280 trees/ha. The three fall-burn units were burned in either September or October of 1993, when buds were set and radial growth was complete. The spring-burn sites were burned on two consecutive days in May 1994, when buds were expanding and trees were actively growing. To avoid high mid-day temperatures, fires were applied during the early morning at temperatures between 10 and 23C, humidities between mid-30 and mid-70%, and wind speeds of less than 8km/hr, using strip head

fires. Fuel loads were generally light, and most litter and much of the woody debris (including slash) were consumed in both the spring and fall burns, with greater woody and forest floor reduction in fall burn units. Fuel moisture contents were generally higher for the spring burns, with the exception of litter, which had higher moisture content in fall burned units due to cool, moist mornings (Harrington 1999b). About 60% of trees between 2 and 18cm DBH (diameter at breast height) were killed in both the fall and spring burned units, mostly due to crown scorch (Harrington 1999a). Only 3% of trees greater than 18cm DBH were dead four years after the fires of both spring and fall burns, and most of the dead trees were smaller than 25cm DBH.

Soil moisture

Soil moisture was measured at 15, 30, and 45 cm depths beneath the surface of mineral soil in 6 plots per unit on five sampling dates throughout summer 2002. We inserted 61cm long, 5cm diameter PVC pipes in the soil in 72 of the 144 plots in the spring of 2001. Soil was removed from the pipe with a soil auger. PVC caps were installed to keep precipitation from entering the pipes. Volumetric percent soil moisture was measured at each depth (15, 30, and 45cm) using time domain reflectometry with a Sentry 200 Troxler (Research Triangle Park, North Carolina) over several sampling dates throughout the field season. In nine plots the granitic sand and rock were hard enough to prevent inserting the PCV to a depth of 45 cm. Therefore there are no data at 45 cm for these plots, although sample size was never reduced to less than 4 per unit.

Tree physiological measurements

For the 2001 field season, six trees within each unit were selected based upon their 1994 post-treatment diameter, crown ratio (the proportion of tree height with live foliage), and degree of fire-induced crown scorch as recorded in a database provided by Mick Harrington (USFS, RMRS Fire Science Laboratory, Missoula, MT). The purpose of non-random tree selection was to reduce the possibly confounding effects of differing tree size or crown scorch on tree response to treatment. Tree selection criteria were: diameter between 25-31cm, a crown ratio between 60-70% and crown scorch levels between 10-20% in burned units. From among these possible trees, six were selected at random for sampling in each unit, with no two trees selected in the same 0.04 ha plot. The same trees were used for physiological measurements in the 2002 research, and are referred to in this paper as "small" trees. In addition to these six trees per unit, two larger trees (DBH 40-50cm) were selected in each unit in 2002 to explore possible tree-size related differences in leaf level photosynthesis, water potential, and resin flow. No two large trees were selected from any one plot. Selection criteria for large trees were less strict than for selection of small trees due to the rarity of large trees across the site; DBH was the primary criterion used.

Predawn water potential (Ψ) was measured from one fascicled bundle of three needles from the six small trees and two large trees in each unit. There were, therefore, 24 trees per unit and 96 total trees measured. Time limitations prevented the completion of all measurements in one morning. Water potential values were measured over the course of three mornings, with each sampling morning consisting of one unit from each treatment. Predawn Ψ values were measured between 12:30 and 5:00 am during two sampling periods in summer, 2002: June 17-19 and July 29-31. Foliage was harvested

using telescoping pruners to remove mid canopy, terminal branchlets. Needle bundles were removed from the branchlet and stored in a sealed, plastic bag with lightly damp paper towels for transport to a work station. Water potential was measured from the fascicular portion of one needle per tree with a PMS pressure bomb (Corvallis, Oregon).

Net photosynthesis was measured in mid-July from 3 small trees and one large tree per unit, with a total of 12 trees per treatment and 48 trees overall measured. The small trees used were the same used in 2001 research. Four trees only were used for these measurements because of time constraints; 2001 results suggested peak performance of pines during late morning and early afternoon. Measurements were taken between 8:30 am and 1:00 pm. Because of the time required to collect these data, measurement were taken over the course of three days such that trees from one unit of all four treatments were measured each of the three days. We used telescoping pruners to harvest sunlit branchlets from mid-canopy on the south side of selected trees. Each branchlet was placed in an unsealed plastic bag with a damp paper towel and kept in the sun to keep it from rapidly desiccating without dramatically restricting gas exchange. Over the course of the three-day sampling period, the weather was consistently clear with minimal day-to-day temperatures variation.

The foliage samples were transported to a work station for gas exchange measurements. 3 bundles (nine needles) were removed from the branch and inserted in the cuvette of a LICOR 6400 Photosynthesis System (Lincoln, Nebraska) to record area-based carbon assimilation (A_{area}). The humidity was controlled to be near ambient conditions, PAR (Photosynthetically Active Radiation: 400-700nm) was controlled at 1000 $\mu mol/m^2/s$ with an external light supply and the carbon dioxide concentration was

controlled at 400ppm from an external supply cartridge. Such conditions were intended to measure gas exchange at near optimal CO_2 and light conditions and mimic conditions used during the 2001 field season. Light intensity, however, was not at saturation levels because of the need to maintain battery power.

To explore possible foliage-age related differences in A_{area}, we measured gas exchange from one, three, five, and either six or seven year-old foliage from each harvested branchlet. Measurements proceeded from youngest to oldest foliage; because field trials at the site suggested a decline in photosynthetic rate in harvested foliage after approximately 10 minutes, measurements of one year old foliage were repeated, whenever possible, after the measurements of the oldest foliage. We found no evidence ($P > 0.5$) for differences between one-year old needle A_{area} measured before and after older age classes. Therefore, the first sampling of one-year foliage is used for analysis in this study.

All 96 selected trees were used to measure the rate of flow of resins following artificial injury. Because temperature may strongly influence the rate of resin flow (Smith 1977), injury was initiated and measurements taken over three days in the same blocks used for Ψ and A_{area} measurements. Trees were injured between 11:00am and 3:00pm using a 2.5cm Osbourne arch punch (Model 149, King Bearing Co., Flagstaff, AZ) to remove bark and phloem and expose the xylem. Previously constructed Aluminum chutes were shaped into the opening in the bark to direct resin into 30 ml graduated collection vials fixed to each tree. The containers were collected 24 hours later (+/- 3 minutes) capped, and returned to the lab for total 24 hour volume measurements. Four

vials failed to capture the resin due to installation error, and one was torn from its tree for unknown reasons. Failed containers were not included in data analysis.

Reproductive output

In late August, when female cones were large and visible on the trees, but had not yet begun to fall to the ground, we conducted a survey of reproductive output across the study site. In all twelve plots per unit (36 per treatment, 144 total) we measured numbers of cones on the ground, numbers of trees with cones, and numbers of cones per tree. Ground cones were measured using a one-meter wide, 20 meter long, east-west transect centered on the plot center. We recorded the number of cones within the transect width of three, visually determined age classes of female cones. Intact, light-colored, strong cones were recorded as "young," darker colored, marginally decadent cones were recorded as "middle," and highly decadent cones were recorded as "old" cones. Every tree within each study plot was surveyed for the presence or absence of mature, female cones. The total number of mature, female cones visible from the east-side of the canopy were counted. Counts were performed for the upper and lower third of the canopy for one small tree and one large tree per plot when available. Cones were counted in a supplemental tree when the first selected tree had no cones, but these supplemental counts were used only in calculations of cone positions in the canopy; analysis of tree-level cone output used only the first, randomly selected trees. Our tree selection for cone counting attempted to approximate criteria used for tree selection in 2001 as closely as possible. We calculated an indicator of cone production per ground area in each unit by multiplying the mean number of trees producing cones per plot by the mean number of cones

produced per tree, as the 25-31 cm DBH trees represent the central tendency of tree diameters in the site. While conducting the cone survey, we also measured the slope at every plot center using a weighted string attached to a protractor.

Female cones were harvested using telescoping pruners during a three-day period in mid-September 2002, when cones were nearly fully mature but not yet releasing seeds. To maximize the number of cones harvested during the three-day period, only cones from the lower and middle portions of the canopy were collected. We collected a variable number of cones from each unit, based upon availability, with the objective of maximizing the number of different trees visited. Whenever possible, at least two cones were collected from both the middle and lower portions of each tree visited. Cones were harvested from between 7 and 15 trees per unit, and brought to the lab in paper bags to be allowed to dry and release seeds.

Several measurements were taken before storing seeds for further analysis. We measured the lengths of all cones, the numbers of cones and seeds in each paper bag (to calculate an average number of seeds per cone for each tree), and the lengths of seed wings from a smaller sampling of cones from each unit. All seeds were floated in a 95% ethanol solution to separate full seeds with well developed embryos, which sank, from seeds with poorly developed embryos, which tended to float. The viable seeds (those that sank in the 95% ethanol) were stratified for 65 days in damp sand at approximately 2C following a 24 hour period of soaking in flushing water.

Seeds were sown in early march, 2003 to measure rates of germination of seeds and growth of seedlings from each treatment. Five trees per unit were selected at random as the sources of stratified seed to be sown. Within the five trees per unit, at least two

were used as sources for mid canopy seeds and two as sources for lower canopy seeds (i.e. seeds from mid and lower canopy positions were represented in each unit and treatment). The only exceptions were for one of the units in the spring burn treatment were only one tree was available as a mid canopy source, and for one of the control units where only one tree was available as a lower canopy source. The number of trees per treatment used as mid and lower canopy sources, respectively were: Control: 9 and 6; Thin: 8 and 7; Spring Burn: 5 and 10; Fall Burn: 7 and 8. Four seeds from each tree were planted in five plastic tree-tubes, for a total of 1200 seeds sown (4 seeds/tube * 5 tubes/tree * 5 trees/unit * 3 units/treatment * 4 treatments). Seeds were sown in a 1:1 mixture of sphagnum peat moss and vermiculite, covered with 0.5cm of vermiculite, and placed in a greenhouse with natural light. All seeds were weighed prior to sowing and their positions in the tree tube were recorded with colored toothpicks. Successful germination was recorded for any seed which emerged from the 0.5cm vermiculite covering within 25 days. As seeds germinated, the date of emergence was recorded and all but one systematically selected seedling per tree-tube was removed, with the objective of growing one seedling per tree-tube for a total of 300 seedlings grown.

Seeds were mist-watered every morning throughout early March. In late March, when most seeds had germinated, watering became less frequent. Tubes were watered to saturation with a dilute (0.3 g/l) solution of Peters brand fertilizer (20-20-20) to provide non-limiting macro and micro nutrients. Seedlings were watered during late March when a sample of tubes dried to 80% of saturated weight. Depending upon weather conditions, watering occurred every second or third morning. An approximately 50mg pellet of slow-release phosphorous fertilizer (46% P_2O_5 available phosphate) was added to each

tube to promote root growth. During April, after successful root growth reduced the risk of drought-induced mortality, watering occurred every third morning. Greenhouse conditions were partially controlled but were strongly influenced by external conditions; to our knowledge, temperatures never fell below 5C or exceeded 25C. All seedlings suspected of fungal infection were removed from the greenhouse to reduce the risk of spreading any contamination.

Several measurements were taken to quantify seedling growth throughout spring 2003. Seventeen days after germination, when minimal additional growth was observed without growth of new needles, we recorded the height to cotyledons and the number of cotyledons for each seedling. Measurements were, therefore, not taken on the same date for each seedling, but rather taken a consistent number of days after germination. Finally, we measured seedling diameter, height, and weight of above and below ground portions of oven dried (60C) seedlings harvested 33 days after germination (i.e. harvesting date varied from seedling to seedling depending on germination date).

Data analysis

The treatments of thinning and prescribed fire were applied to the site units, not to the individual sampling plots. To avoid pseudoreplication, all measurements taken within a unit (at the plot-level) were considered sub-samples and the unit means were considered the ultimate sample, such that n=3 per treatment for all dependent variables considered. Treatment differences of most dependent variables were analyzed using one-way ANOVA (with 4 levels). Two-way ANOVA was used for dependent variables involving measurements in trees of different size, or at different canopy positions. Non-significant

interaction terms were dropped from the final analyses. Tree size category was not significant in most response variables, and data were grouped by unit and analyzed using one-way ANOVA. Least Significant Difference (LSD) posteriori test was used for multiple mean comparisons. Water potential data and soil moisture data were also analyzed using a one way Repeated Measures ANOVA, with treatment as a factor. Pearson correlation analyses were used to determine inter-relationships among measures of tree performance from both 2001 and 2002. We used July measurements of physiological activity because this allowed us to compare the several parameters from the same time of year. Correlation analyses were also used to explore inter- relationships among individual seed characteristics and seedling growth measurements. We used 2-tailed tests because the direction of possible relationships was not in all instances predictable. Differences were determined significant at the $\alpha = 0.05$ level, although differences significant at $\alpha = 0.1$ are also reported. All response variables measured in this study displayed normal distributions. Two soil moisture measurements (of 15 total) failed to satisfy homogeneity of variance assumptions, but all were analyzed assuming equal variance. Unless noted, all other variables displayed homogeneity of variance.

Results

Basal area and tree density in all actively managed treatments 9 years after treatment implementation were still lower relative to the control (Table 1). Basal area and tree density was similar in all actively managed stands. In spite of reductions of basal area and tree density, average tree DBH nine years after treatment implementation did not differ between treatments (overall average of 28.5 cm; Table 1).

There were no differences due to treatment in soil volumetric water content throughout the season at any depth measured. Soil moisture content was higher at greater depths throughout the season. All depths displayed decreasing water content through the summer until September rains brought some recovery of soil moisture levels (Figure 1).

Predawn Ψ values did not differ significantly on either sampling date between large and small trees in any treatment; $\Psi_{predawn}$ data were therefore analyzed with large and small tree data pooled for unit means. $\Psi_{predawn}$ values were significantly lower in trees of control units than in all other treatments ($F = 10.66$, $P_{treatment} < 0.01$, Figure 2). There were no differences in $\Psi_{predawn}$ between thin, spring burn, and fall burn trees. $\Psi_{predawn}$ values declined significantly between the June and July sampling periods ($F = 342.95$, $P_{date} < 0.001$) and there was a significant ($F = 14.68$, $P < 0.01$) treatment x date interaction due to greater declines in $\Psi_{predawn}$ in control trees (Figure 2).

Photosynthesis rates decreased significantly with needle age ($F = 31.74$, $P < 0.001$; Figure 3). We found no evidence that A_{area} differed due to treatment, nor was there a significant date x treatment interaction. However, there was moderate evidence (t test, $P < 0.1$) that one year old needles had higher rates of photosynthesis in burned units relative to thin-only and control units. As with $\Psi_{predawn}$, A_{area} did not vary with tree size.

We found no evidence for differences in resin flow rates due to treatment or tree size (Table 2). Resin volumes were highly variable, ranging from 1ml to 31ml of resin released from the wound in a 24 hour period.

The percentage of trees bearing cones tended to be lower in the control treatment relative to al other treatments, although only differences between control and fall burn (which showed the highest mean) were statistically significant ($P<0.05$; Figure 4). There

were no significant differences between treatments in the young and middle age classes of cones on the ground, although treated units had higher means (Figure 4). The slope of the terrain was significantly higher in both burned units relative to control units, and significantly higher in spring-burn units than in thin-only units ($F = 7.31$, $P < 0.05$, Table 2), but when slope was included as a covariate in the ANOVAs for cone numbers on the ground, treatment was still not a significant factor. There were significantly more old, decadent cones in the thin-only and control units relative to both burned units ($F = 8.887$, $P < 0.01$, Figure 4).

Analysis of cone production on individual trees using randomly selected trees shows greater reproductive output of trees in treated units relative to trees in control units (Figure 5). In the large trees (>40cm DBH) sampled, we found significantly higher numbers of cones per tree in fall burn units relative to control units ($F = 12.79$, $P < 0.01$, Figure 5), with all other between treatment differences not significant. In the far more common smaller size classes (25-31cm DBH) we found significantly higher numbers of cones per tree in treated units relative to control units ($F = 4.74$, $P < 0.05$, Figure 5), and no significant differences among treated units. The calculated indicators of cone production on a ground area basis in each unit provide evidence for significantly higher cone production in treated units than in control units ($F = 6.79$, $P < 0.05$, Figure 5). The proportion of cones in small trees found in the upper half of the canopy was significantly lower ($F = 6.15$, $P < 0.01$) in spring burn trees relative to all other treatments (Figure 5).

Comparison of selected tree-level measurements from 2001 and 2002 revealed evidence for several significant correlations (Table 3). July 2002 $\Psi_{predawn}$ was positively correlated with July 2001 A_{area} ($P < 0.05$), the proportion of foliage composed of young

foliage ($P < 0.01$), cone production ($P < 0.01$), and tree diameter ($P < 0.01$). July 2001 A_{area} was positively correlated with July 2002 A_{area} ($P < 0.05$) and young foliage ($P < 0.05$). Twenty-four hour resin flow rates were positively correlated only with tree diameter ($P < 0.05$). Cone production was also positively correlated with tree diameter ($P < 0.05$). The basal area in the vicinity of sampled trees was negatively correlated with July 2002 $\Psi_{predawn}$ ($P < 0.001$), young foliage ($P < 0.001$), and cone production ($P < 0.05$).

While control trees had slightly longer cones than trees in the thin and spring burn units ($P_{treatment}<0.05$), the mean number of total and filled seeds per cone did not differ significantly between treatments (Figure 6). However when treatments were divided into burned (spring and fall burning combined) and unburned (control and thin combined) the percentage of filled seeds per cone was greater in the burned treatments (79.58±1.97 SE and 70.9±3.47 SE for burned and unburned treatments, respectively; $P_{treatment} = 0.05$) while seed mass was greater in the unburned treatments (54.8±1.16 SE and 59.3±1.09 SE for burned and unburned treatments, respectively; $P_{treatment} =0.01$). However, lower seed mass in burned relative to unburned treatments were largely due to lower seeds mass in the spring burn treatment, which differed significantly from all other treatments ($P_{treatment} = 0.002$; Figure 6). Seed wing length did not differ between treatments (data not shown). Cone length, number of seeds per cone, and percent viable seeds tended to be greater at lower canopy positions relative to middle canopy positions (P ranged between 0.05 and 0.08 in all cases; Table 4). Correlation analyses using individual trees provide evidence for positive correlations between the length of cones with the seed wing length, the number of seeds per cone, and the mass of individual, viable seeds ($P < 0.001$, Table 5).

There was also a positive correlation between the percentage of viable seeds and the number of seeds per cone ($P < 0.001$, Table 5).

Analysis of the seeds used for the germination experiments randomly sampled from the larger pool of harvested seeds revealed significant differences due to treatment in germination rates and growth of seedlings (Figures 7 and 8). The overall rate of germination within 25 days was 82.1%, occurring at an average of 12.1 days after sowing. Although seed mass was not a significant factor determining germination success in this study, the mean mass of germinating seeds (82.6 mg) was higher than non-germinating seeds (81.9 mg). In only 12 of the 300 tubes in which seeds were sown none of the four seeds sown per tube germinated within 25 days. Ten of these 12 tubes were from two trees, both from spring-burn units. Two seedlings died for unknown reasons, and 10 more were removed from the growing racks and from final seedling growth measurements due to possible fungal infection (most likely of the genus *Fusarium*). Therefore, the 17-day cotyledon measurements included 288 seedlings and the final, 33-day, measurements of seedling growth included 276 seedlings. Because seeds used for the greenhouse experiment were stratified and subjected to circulating water prior to sowing and weighing, seed mass was higher (due to water absorption) than that of all seeds harvested in the field. As for the larger data set (Figure 6), mass of seeds used for the germination experiment was lower in the spring burn treatment, although differences were no statistically significant (Figure 7). Spring burn seeds, however, exhibited significant lower germination rates ($F = 5.71$, $P_{treatment} < 0.05$) relative to all other treatments and longer time to germination (Figure 7). Consistent with these results, spring burn seedlings tended to be smaller than all other treatments (Figure 8), although

differences were only statistically significant for stem diameter (spring burn seedlings had lower values than fall burn and control; $P < 0.01$) and for shoot and total biomass (spring burn seedlings were smaller than fall burn seedlings; $P = 0.05$; Figure 8).

In contrast to spring burn seeds, fall burn seeds tended to produce larger seedlings with marginally greater number of cotyledons relative to thin only and control units ($P=0.08$), significantly larger diameters than spring burn and thin seedlings ($P < 0.01$) and significantly greater total biomass relative to spring burn units (see above). Root dry weight biomass, shoot to root biomass ratio, shoot height and height to cotyledons did not differ among treatments (Table 6).

Time to germination was significantly longer for seeds from the lower canopy (Table 7). The two-way ANOVA did not reveal canopy position differences for any of the other variables analyzed (Table 7).

We found strong correlations between seed mass and important measures of seedling growth. Overall, seed mass was positively correlated with the final shoot height, diameter, and seedling dry weight biomass ($P < 0.001$ for each, Table 8). Interestingly, while the time to germination was negatively correlated with height ($P < 0.001$) and seedling biomass ($P < 0.05$), it was positively correlated with seed mass and diameter ($P < 0.001$ for both, Table 8). ANOVA of the final total dry weight of all grown seedlings with the individual tree as a factor revealed strong evidence ($F = 5.44$, $P < 0.001$) for significant differences in seedling biomass depending on the individual tree source of seeds.

Discussion

In a previous study at the Lick Creek Experimental Site we showed that active management by thinning or thinning followed by spring or fall prescribed burning improved the physiological performance of second growth ponderosa pine relative to trees in unmanaged stands with higher basal area (Peters et al. *submitted*). However, we found no evidence that long-term physiological performance was affected positively or negatively by the application of either spring or fall prescribed fire relative to thinned stands. Results from this study corroborate our previous finding that active management of second growth ponderosa pines by either thinning or thinning followed by prescribed burning improves tree water status. Consistent with our previous results we also found that cone production in trees between 25 and 31 cm in DBH is significantly higher in trees from actively managed stands. In this study we were particularly interested in analyzing the effect of the specific active management practice on resin flow and reproductive output. While resin flow did not vary across treatments (including control), field and greenhouse observations suggest that some reproductive traits vary depending on the specific active management treatment. Overall, trees subjected to either spring or fall burning produced cones with higher number of total and filled seeds relative to trees in control and thin treatments. We also found that cones of trees subjected to thinning followed by spring burning produced significantly smaller seeds (lower mass) relative to all other treatments. Consistent with our field results, greenhouse studies revealed that filled seeds from the spring burn treatment exhibited significantly lower germination rates relative to all other treatments and tended to produce smaller seedlings (although differences were only significant between spring burn and fall burn treatments). These

results suggest that the specific management treatment may have implications on reproductive output traits and long-term recruitment of second growth ponderosa pine. To our knowledge this is the first time where management-induced differences in reproductive output have been documented for ponderosa pine. Because this is a case study and results may be dependent on the specific conditions under which management is applied, it is premature to extrapolate potential broad implications of the findings reported here. However, the sole fact that some reproductive traits appear to be sensitive to specific management practices is an important finding that, if corroborated by further studies, has many potential important implications for ecological restoration.

Results from 2002 were, for the most part, consistent with our previous findings and the conclusion that reductions in basal area in actively managed units ameliorated physiological performance and growth of second growth ponderosa pine in spite of no apparent differences in soils resource availability (Peters 2002): we in creased reproductive output and improved water status of trees in treated units relative to control units although soil moisture content did not vary between control and treated units.

Significantly higher July 2002 $\Psi_{predawn}$ in treated units is consistent with higher early-morning Ψ during the summer of 2001 in treated units. The positive correlations among 2002 $\Psi_{predawn}$, 2001 A_{area}, and the proportion of younger foliage, along with negative correlations between these parameters and surrounding basal area (competition) suggest that increased competition for water in control units limits photosynthesis and growth. Previous studies have also shown than A_{area} is determined to a large degree by tree water status (Zhang et al. 1997, Dang et al. 1997, Panek and Goldstein 2001). Basal area reduction frequently improves growth of ponderosa pine because of the release from

competition (Fiddler et al. 1989, Arno et al. 1996). Photosynthesis measurements indicated that the decline in A_{area} with increasing needle age was similar in all treatments. The lack of evidence for a treatment x needle age interaction suggests that control trees do not compensate for lower relative A_{area} in young needles with higher relative A_{area} in older needles. In contrast with our measurements in June 2001 A_{area} in July 2002 was not lower in control units. However, consistent with our 2002 measurements, A_{area} in late July 2001 was also similar in all treatments, suggesting that stomatal closure later in the summer may equally limit photosynthesis in all treatments. In contrast with other studies (Yoder et al. 1994) we did not find tree size-related differences in $\Psi_{predawn}$ or A_{area}. However, our method of harvesting foliage using pruners prevented sampling foliage from the upper portion of large tree canopies where differences may be more apparent.

Recent studies have shown increased rates of resin flow following prescribed fire in ponderosa pine in the short term (Feeney et al. 1998), and scorched boles have been shown to increase resin flow in individual red pines (*Pinus resinosa*), possibly reducing the probability of post-fire beetle kill (Santoro et al. 2001). Although our measurements of resin flow were highly variable and collected only once, our findings suggest that if fire application increased resin flow at Lick Creek, this increase was short lived. While our ANOVA analysis suggested that tree size did not influence resin flow, we found a significantly positive correlation between tree diameter and resin flow. We suspect that this discrepancy is due to differences in statistical power between the two analyses (lower with the ANOVA were n= 12 and higher with the correlation analyses were individual trees were used) and that resin flow is ultimately related to tree diameter. Although average tree DBH and age class distribution (data not shown) nine years after treatment

implementation was similar in all units, previous results showed that radial wood increment after treatment implementation was lower in control trees (Peters 2002). If active management results in an increase in tree diameter in the long term, our results suggest that these trees may be able to produce more resin and be better defended.

Cone production on an individual tree basis was much lower in control trees relative to all other treatments, which is consistent with the general improvement of physiological performance following active management (Peters et al. *submitted*). The significant positive correlation between tree water status and cone production and the negative correlation between cone production and basal area surrounding the measured tree suggests that higher competition for water in control treatments has a negative effect on cone production. Karlsson (2002) also found improved reproductive output following basal area reduction treatments. Higher tree density in control units did not offset such low cone production and cone production per unit ground was still lower in control treatments. As with resin flow, cone production increased with tree size.

Interestingly, cones from control treatment tended to be longer than in any other treatment (differences only significant with respect to thin and spring burn cones). However, the number of seeds per cone and the percent of viable seeds did not vary among treatments. A tendency for increased cone size in control trees may have resulted from the lower cone production (i.e. less cones allowed for a slight increase of size in the remaining cones). However, higher competition in control units relative to all other units due to higher basal area and tree density apparently prevented control trees to produce more seeds per cone and larger seeds. The fact that overall cone size was positively related to number of seeds per cone and higher individual seed mass, and that control

cones did not follow such general trends suggests that resources may have limited seed number and mass in control trees. While cone production was higher in trees from treated stands we did not find significantly higher number of young and middle aged cones on the ground in treated units relative to the control treatment, even when correcting for the slope effect. Ponderosa pine exhibits a cyclic-like reproductive cycle with periodical mast cone production years (between 7 and 11 years) followed by low or intermediate cone production years. 2002 was a high production year, although we lack the necessary data to verify that it was a truly mast year. It is possible that recent, less productive years may have had insufficient cone production to reveal the treatment differences apparent in 2002 based on cone counts per tree. Lower density of old, decadent cones in burned units reflect the consumption during prescribed burning.

Our results suggest that some reproductive traits are influenced by the specific management practice. When treatments were designated as burned (fall and spring prescribed burning combined) or unburned (control and thin combined) we found that trees in the burned treatment tended to produce cones with more seeds and with a greater percentage of filled seeds in spite of the fact that cone length did not vary between burned and unburned treatments. We do not know the reason for this difference but we speculate that 2002 was the first mast cone production year after prescribed burning in the fall 1993 and spring of 1994 (i.e. nine growing seasons). If so, prescribed fire may have stimulated in some yet unknown way quantitative seed output per cone. In spite of fire-induced differences in seed output per cone, the specific time of prescribed fire apparently had a stronger effect on seed quality (see below).

Perhaps the most interesting results from this study are the fact that the seed mass from harvested field cones and germination rates of spring burn seeds sown in the greenhouse were significantly lower than in any other treatment. Such traits were related with higher time to germination and with a tendency for overall smaller seedlings. While many of these differences were not striking (statistically significant differences were apparent only with respect to certain treatments) they were all very consistent. We also caution that our statistical analysis is very conservative because we used the unit means (n=3 per unit) rather than individual plots or trees sampled per unit. The increase in time to germination in the smaller spring burn seeds is inconsistent with the overall positive correlation between seed mass and time to germination, which suggests that spring burning had a negative effect on seed quality.

In contrast with spring burn seeds, fall burn seeds tended to be heavier and to produce larger seedlings. As for spring burn seeds, differences were small and often only statistically significant relative to certain treatments. However, they were also very consistent. Fall burn slightly increased cone production per ha as well as the proportion of cone-bearing trees (although differences were statistically significant only with respect to the control) and large fall burn trees exhibited significantly higher number of cones relative to all other treatments. These results suggest that fall burning improved reproductive output in ponderosa pine. Overall our results suggest that fall burn may improve reproductive output but that spring burn decreases seed quality relative to all other treatments including the control. To our knowledge this is the first study suggesting that reproductive output in ponderosa pine may be sensitive to burning treatments and the specific time of burning. What factors could explain these differences? To our knowledge

very few studies have analyzed functional and physiological responses of trees to prescribed burning. Our previous results suggested that physiological performance of ponderosa pine was not affected by the specific active management treatment (Peters et al *submitted*). Other studies, in contrast, have documented a reduction in ponderosa pine performance induced by spring fire (Grier 1989, Busse et al. 2000). Historically, ponderosa pine systems in the northern Rocky Mountains occurred in late summer and fall when fuel moisture was low and lightning activity was greatest. The prescribed spring burning in this study was implemented in May when soil moisture is greatest and root growth is also greatest (Grier 1989). It is possible that damage to fine roots due to spring burning had a negative effect on the quality of seeds produced during the first episode of mast cone production in 2002. Fall burning, in contrast, may not have had such a negative effect on seed quality due to the temporary pulse of nutrients induced by fire (Covington and Sackett 1984) which may have been enhanced by the fire-induced mineralization of already decaying fine roots in the fall. Such nutrients may stimulate fine root production and nutrient acquisition in fall burn trees during the first spring following fire and may contribute to reproductive cues for future mast production of cones. The duration of the apparent effect of prescribed fire on reproductive traits is not known. It is also not known whether such effect is consistent at the landscape level. If so, it may influence ecological restoration goals by potentially changing seedling recruitment and establishment (see below) and food quality and quantity available to predators.

Consistent with previous research (Setterington and Keppie 1997) cone length was positively correlated with the number of seeds per cone and the mass of filled seeds. We also found that seed mass was positively correlated with seedling height, stem

diameter and total biomass as well as with time to germination. Several studies have shown positive correlations between seed mass and seedling success in pines, including rates of germination (Suprr 1944, Dunlap and Barnett 1983) and seedling growth (Griffin 1974, Linhart and Mitton 1985, Surles et al. 1993). Higher seed mass reflects a greater embryo size with more resources for initial growth. Higher quality seeds have been shown to have higher first year survival (Winsa and Bergsten 1994) and high relative growth (Righter 1945; Robinson and van Buijtenen 1979, Surles et al. 1993). Growth stimulation in pines grown from heavier seeds may persist for up to 15 years (Robinson and van Buijtenen 1979, Surles et al. 1993) although a much shorter persistence for the relationship between seed size and tree growth has also been reported for pines (Righter 1945). While overall, our results also show that heavier seeds take slightly longer to germinate but they mature into superior seedlings, a significant exception were the lighter seeds from the spring burn treatment, which took longer to germinate but tended to produce smaller seedlings. Such exception is again consistent with a decrease in seed quality in spring burn seeds. We did not find differences in shoot to root ratio among treatments. This trait has been involved in drought survival (Cregg 1994) but variability is more likely controlled by environment and genetics than maternal resource investment in seeds (McMillin and Wagner 1995). Therefore, lack of differences in our study is not surprising given the repeated watering and fertilization of the seedlings.

Results reported here have potentially important implications for ecological restoration: prescribed burning in lower elevation ponderosa pine systems of the interior northwest is usually implemented in the spring because of the risk associated by burning in the fall when fuels are dry. While very few studies have examined differential

individual responses to spring and fall burning and our previous work indicates no significant differences in physiological performance (Peters et al. *submitted*) results here and previous research examining tree growth responses as a function of seed size (see above) suggest that spring burning may have negative consequences on seed quality and future seedling growth and that fall burning may increase reproductive output and seed quality. Because recurrent natural fire in ponderosa pine systems of the interior northwest occurred in the fall, a tendency for a higher reproductive performance of second growth trees in the fall prescribed burning may have an evolutionary basis.

If the sole management goal was to reduce forest density, potential negative effects on reproduction of spring burning may be advantageous in the long term as they may slow down future recruitment and reduce the need of repeated management. However, decreases in seed quality may have negative consequences on seed predators and therefore not be desirable from an integrative ecological management perspective.

Overall canopy position had a minor effect on cone size, number of seeds per cone, percentage of viable seeds and seed mass. Only time to germination was significantly longer for lower canopy seeds, which is consistent with the fact that mean seeds mass tended to be higher (although not significantly so). Such small differences may relate to changes in light availability, resource allocation, foliage age, and branch level physiological activity in different canopy positions (Watson 1986). Seki (1994) proposed that reproductive output at a particular canopy level in *Abies mariesii* depended upon the dry matter accumulation of the tree at that level rather than in the whole tree.

In conclusion, results from this study show that active management of second growth ponderosa pines by either thinning or thinning followed by prescribed burning

improves tree water status and cone production. We also found that some reproductive traits vary depending on the specific active management treatment. While burning may influence the number of filled seeds per cone, the specific time of burning appears to have a stronger effect on seed quality and subsequent seedling growth with the lowest performance associated with spring burning). If corroborated by other studies, the findings reported here suggest negative fitness consequences due to spring prescribed burning. Such conclusions would have important implications for ecological restoration.

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Table 1. Basal Area (BA), tree density and average tree DBH in each treatment.

	treatment			
	control	thin	spring-burn	fall-burn
BA (m^2/ha)	29.4(1.86)a	16.3(0.58)b	13.5(1.16)b	16.8(0.95)b
Density (Trees/ha)	373.2(50.21)a	182.6(17.7)b	232.2(22.8)b	207.1(12.7)b
DBH (cm)	28.3(1.13)	29.7(1.35)	28.09(1.20)	29.19(1.27)

Data are means (standard errors); within a row, data followed by different letters differ at $P < 0.05$

Table 2. Twenty four hour resin flow and slope of the terrain in each treatment.

	treatment			
	control	thin	spring-burn	fall-burn
Resin flow (ml)	9.88(0.90)	7.52 (1.52)	9.68(1.48)	8.43(2.23)
Slope (degrees)	13.42(1.23)a	16.00(0.80)ab	20.30(0.72)c	16.92(1.32)bc

Data are means (standard errors); within a row, data followed by different letters differ at $P < 0.05$

Table 3. Pearson's correlation values and significance levels of July 2001 and 2002 tree performance measurements with 2002 cone production, and surrounding basal area (tree competition). Physiological measurements were taken for 36 total trees, other measurements for 72 trees.

		July, 2002 $\Psi_{predawn}$	July, 2001 A_{area}	July, 2002 A_{area}	Resin flow	Young foliage %	Cone output	DBH	Basal Area
July, 2002 $\Psi_{predawn}$	Pearson r	1.000	**.295**	.157	-.093	**.329**	**.415**	**.324**	**-.589**
	P	.	**.041**	.187	.228	**.002**	**.006**	**.003**	**.000**
July, 2001 A_{area}	Pearson r		1.000	**.316**	-.053	**.326**	.306	.210	-.193
	P		.	**.034**	.385	**.026**	.089	.109	.130
July, 2002 A_{area}	Pearson r			1.000	.094	.161	.339	.179	-.232
	P			.	.308	.181	.078	.156	.093
Resin flow	Pearson r				1.000	.017	-.184	**.251**	.012
	P				.	.445	.153	**.021**	.462
Young foliage %	Pearson r					1.000	.122	.091	**-.406**
	P					.	.240	.225	**.000**
Cone output	Pearson r						1.000	**.309**	**-.387**
	P						.	**.033**	**.010**
DBH	Pearson r							1.000	-.162
	P							.	.088
Basal Area	Pearson r								1.000
	P								.

Table 4. Cone and seed measurements based upon the position in the tree canopy of cone harvest (all treatments combined).

Canopy Position	Cone length (cm)	Seeds/ cone	Viability (%)	Seed mass(mg)	Seed wing length(cm)
Lower	8.99(0.21)+	83.02(2.83)+	82.45(7.11)+	63.7(2.72)	2.01(0.03)
Middle	8.03(0.03)+	59.42(2.04)+	61.08(7.68)+	58.0(1.70)	2.11(0.04)

Data are means (standard errors); within a column, data followed by + differ at $P < 0.08$

Table 5. Pearson's correlation values and significance levels for correlations between cone and seed measurements (all harvested cones).

		Cone length (cm)	Viability	Viable seed mass	Seeds per cone	Wing length
Cone length	Pearson r *P*	1.000 .	.076 .329	**.349** **.000**	**.502** **.000**	**.541** **.000**
Viability	Pearson r *P*		1.000 .	-.041 .601	**.318** **.000**	-.104 .518
Viable seed mass	Pearson r *P*			1.000 .	.008 .923	.035 .826
Seeds per cone	Pearson r *P*				1.000 .	.125 .436
Wing length	Pearson r *P*					1.000 .

Table 6. Seedling growth measurements for all seedlings grown in each treatment.

	treatment			
	control	thin	spring-burn	fall-burn
Height to Cotyledons (cm)	3.77(0.12)	3.90(0.20)	3.79(0.17)	3.81(0.09)
Shoot biomass (g)	79.1(5.03)ab	80.3(4.01)ab	75.0(1.82)a	87.5(2.35)b
Root biomass (g)	31.4(1.67)	30.0(0.62)	30.6(1.28)	33.1(0.89)
Shoot/Root biomass	2.60(0.05)	2.74(0.08)	2.55(0.12)	2.67(0.06)

Data are means (standard errors); within a row, data followed by different letters differ at $P < 0.05$

Table 7. Seed mass, time to germination, and selected seedling growth measurements based on canopy position of cone source (all treatments combined).

Canopy Position	Seed mass (mg)	Days to germination	Diameter (mm)	Height (cm)	Total dry weight (mg)
Lower	86.3(12.07)	13.1(0.28)*	1.24(0.04)	7.69(0.46)	106.1(13.07)
Middle	80.7(2.90)	11.9(0.23)*	1.16(0.01)	8.56(0.15)	114.6(2.30)

Data are means (standard errors); within a column, data followed by an asterisk differ at $P < 0.05$

Table 8. Pearson's correlation values and significance levels for correlations between seed mass, germination time, and seedling growth measurements of all seedlings grown.

		Seed mass	Days to germinate	Height	Diameter	Total dry weight
Seed mass	Pearson r *P*	1.000 .	**.220** **.000**	**.250** **.000**	**.479** **.000**	**.547** **.000**
Days to germinate	Pearson r *P*		1.000 .	**-.227** **.000**	**.342** **.000**	**-.120** **.047**
Height	Pearson r *P*			1.000 .	.072 .231	**.650** **.000**
Diameter	Pearson r *P*				1.000 .	**.333** **.000**
Total dry weight	Pearson r *P*					1.000 .

Figure Captions

Figure 1. Volumetric soil moisture content at 15, 30, and 45cm depths through the 2002 field season in all four treatments. Error bars represent one standard error of the mean.

Figure 2. Predawn water potential values of sampled trees in each treatment on two sampling dates. Error bars represent one standard error of the mean.

Figure 3. Photosynthesis rates of different needle age classes in each treatment. Error bars represent one standard error of the mean.

Figure 4. Percent of cone bearing trees (upper panel), young (shaded bars) and medium (white bars) cones per ha (middle panel) and old cones per ha (lower panel). umber of cones per tree (upper panel), proportion of cones in the upper canopy (middle panel) and estimated cones /ha (lower panel) in each treatment. Different letter denote statistically significant differences between treatments ($P < 0.05$).

Figure 5. Number of cones per tree (upper panel), proportion of cones in the upper canopy (middle panel) and estimated cones /ha (lower panel) in each treatment. Shaded and white bars in upper panel are data for small (25-31 cm DBH) and large trees (> 40 cm DBH), respectively. Different letter denote statistically significant differences between treatments ($P < 0.05$).

Figure 6. Cone length, seeds per cone, filled seeds per cone and filled seed mass in the different treatments. Different letter denote statistically significant differences between treatments ($P < 0.05$).

Figure 7. Seed mass, percent germination and time to germination of seeds from each treatment sown in the greenhouse. Different letter denote statistically significant differences between treatments ($P < 0.05$).

Figure 8. Number of cotyledons, final height, basal diameter and total biomass of seedlings grown in the greenhouse from seeds from each treatment. Different letter denote statistically significant differences between treatments ($P < 0.05$).

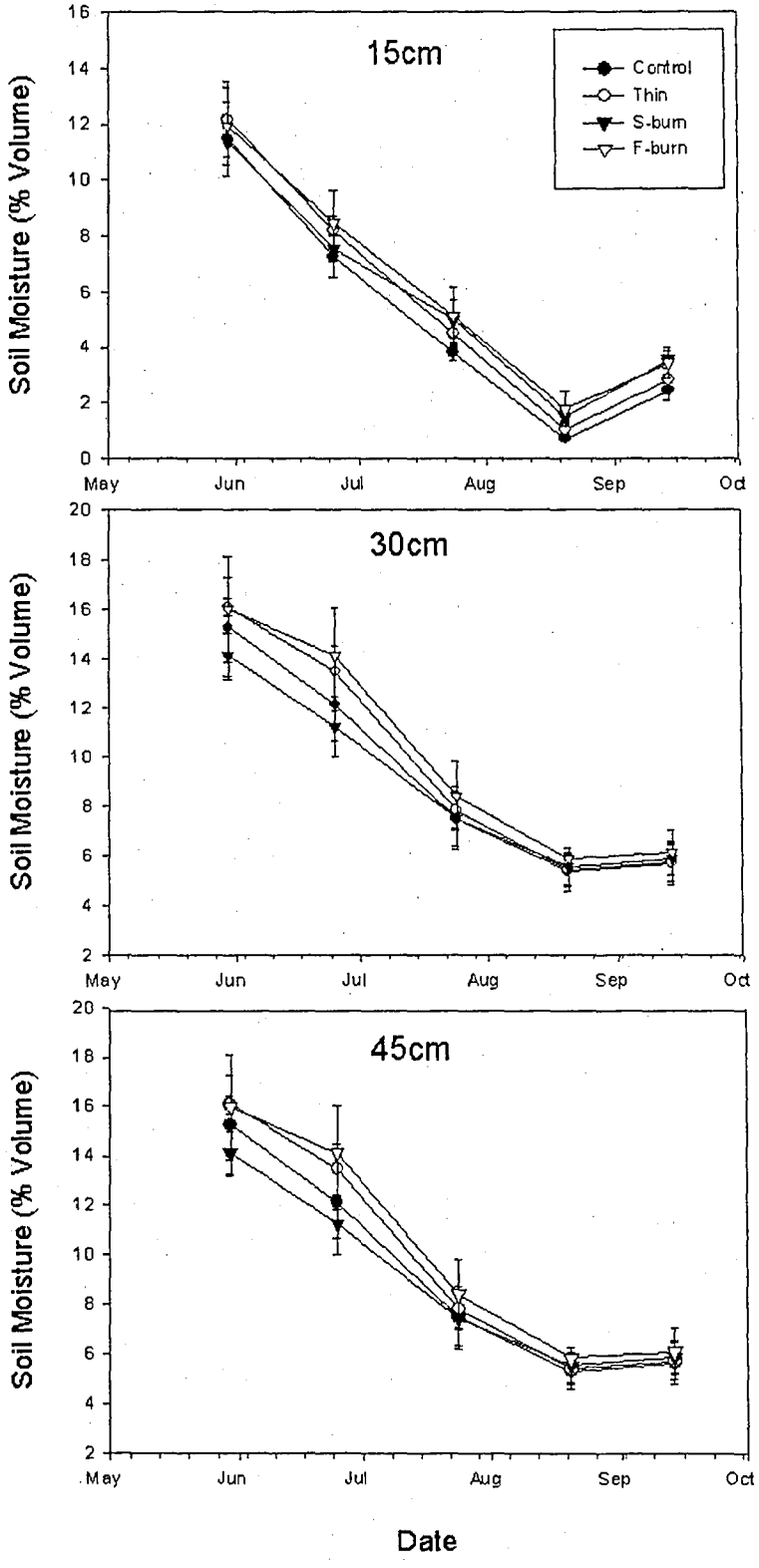
15cm
30cm
45cm
Control
Thin
S-burn
F-burn
Soil Moisture (% Volume)
Soil Moisture (% Volume)
Soil Moisture (% Volume)
May
Jun
Jul
Aug
Sep
Oct
Date

Figure 1

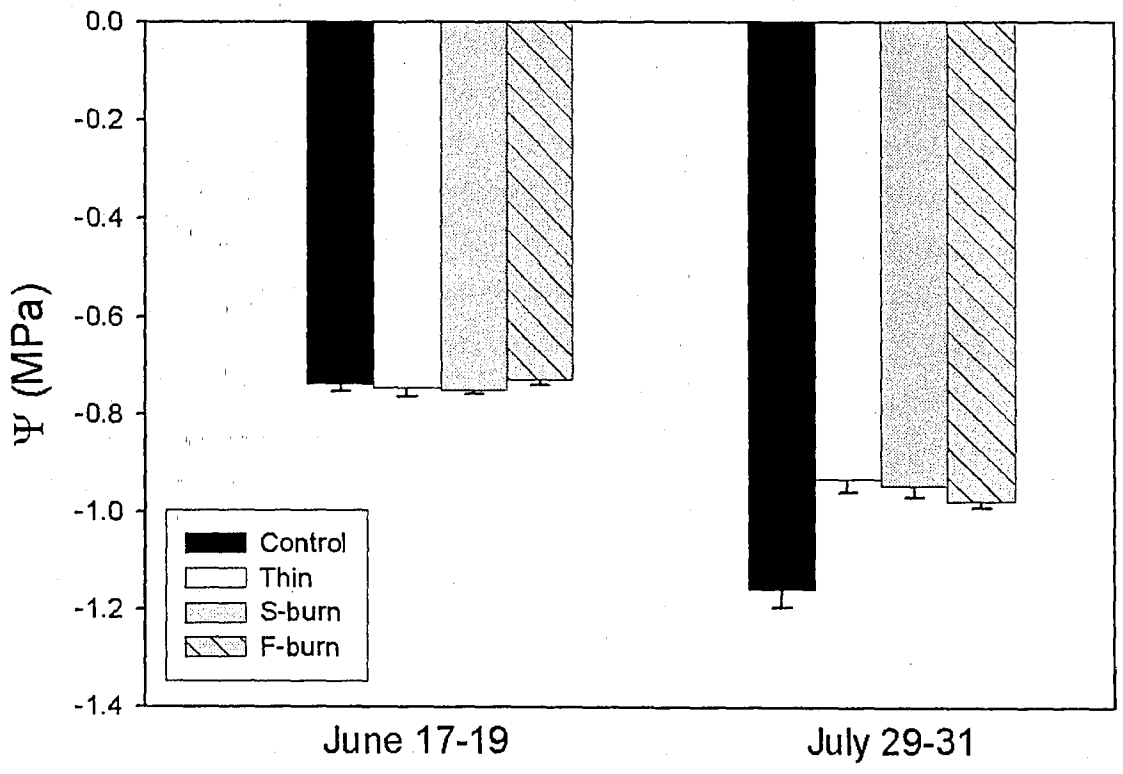
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
-1.4
Ψ (MPa)
Control
Thin
S-burn
F-burn
June 17-19
July 29-31

Figure 2

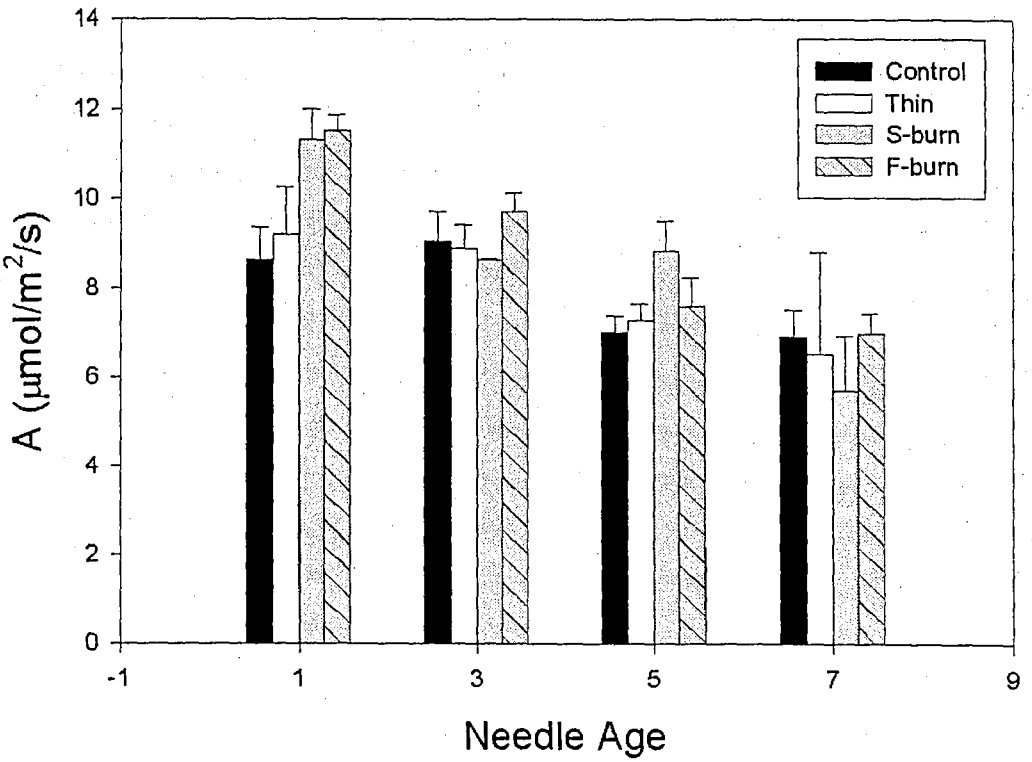
14
12
10
8
6
4
2
0
A (µmol/m²/s)
-1
1
3
5
7
9
Needle Age
Control
Thin
S-burn
F-burn

Figure 3

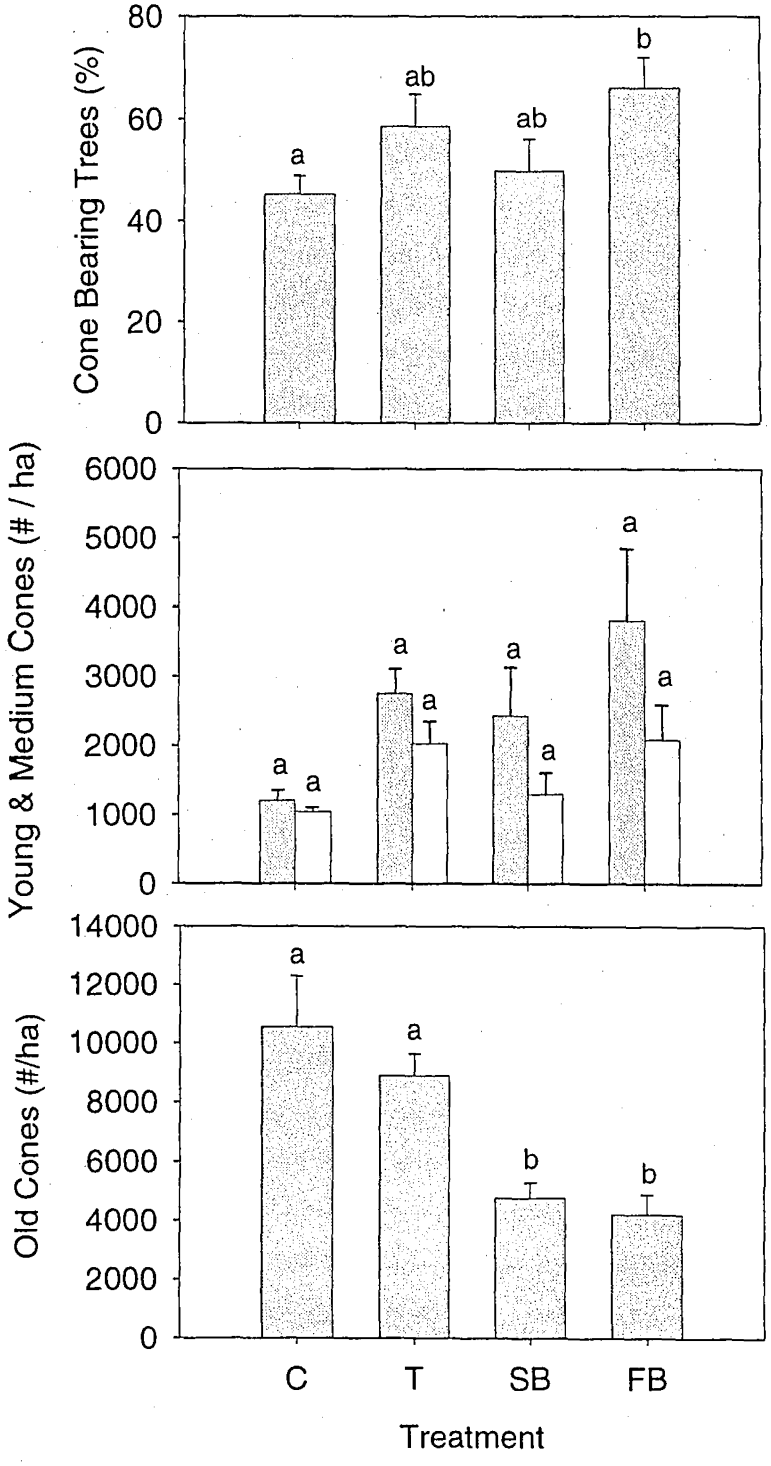
Cone Bearing Trees (%)
80
60
40
20
0
a
ab
ab
b
Young & Medium Cones (# / ha)
6000
5000
4000
3000
2000
1000
0
a
a
a
a
a
a
a
a
Old Cones (#/ha)
14000
12000
10000
8000
6000
4000
2000
0
a
a
b
b
C
T
SB
FB
Treatment

Figure 4

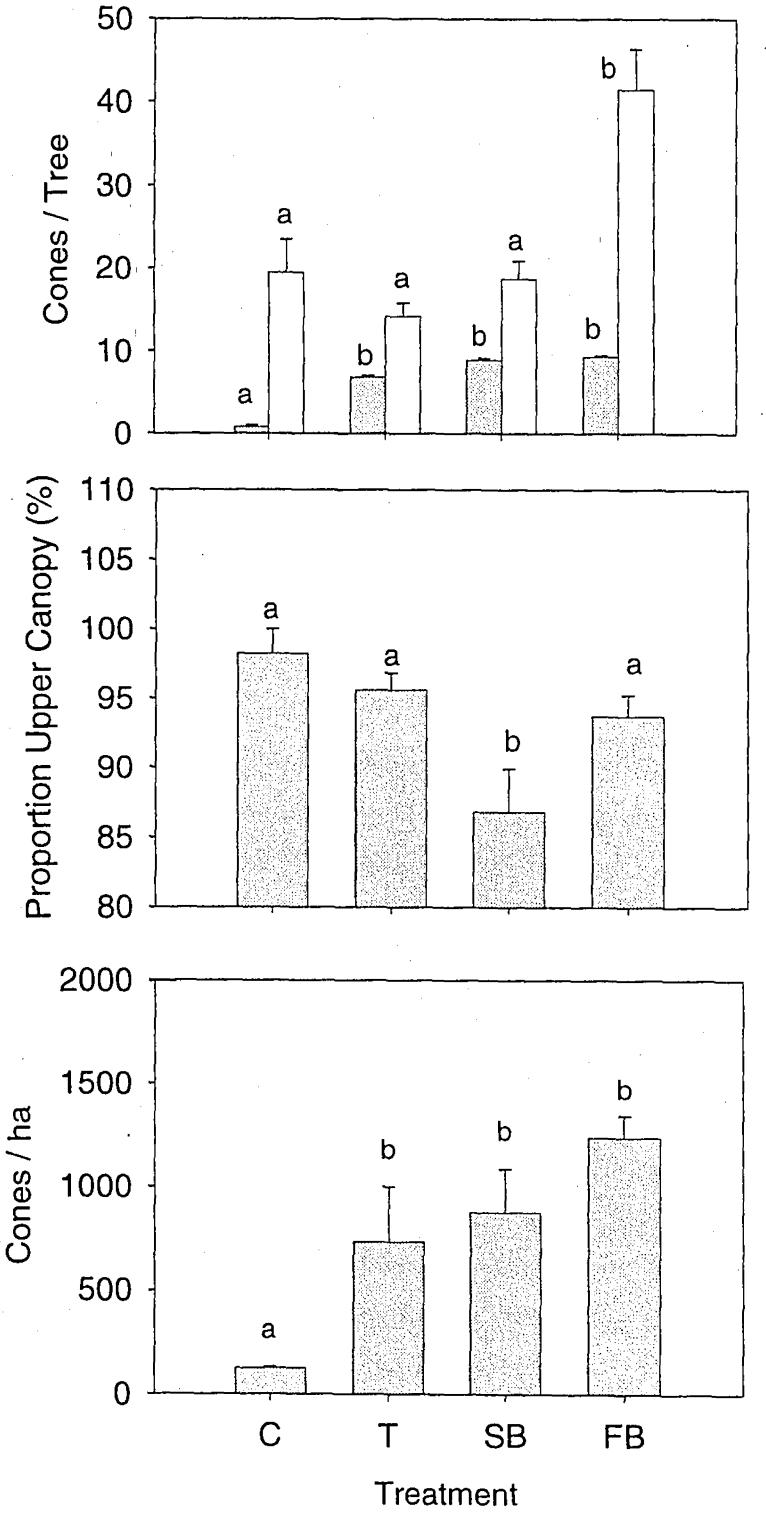
Cones / Tree
50
40
30
20
10
0
a
a
b
a
a
b
b
b
Proportion Upper Canopy (%)
110
105
100
95
90
85
80
a
a
b
a
Cones / ha
2000
1500
1000
500
0
a
b
b
b
C
T
SB
FB
Treatment

Figure 5

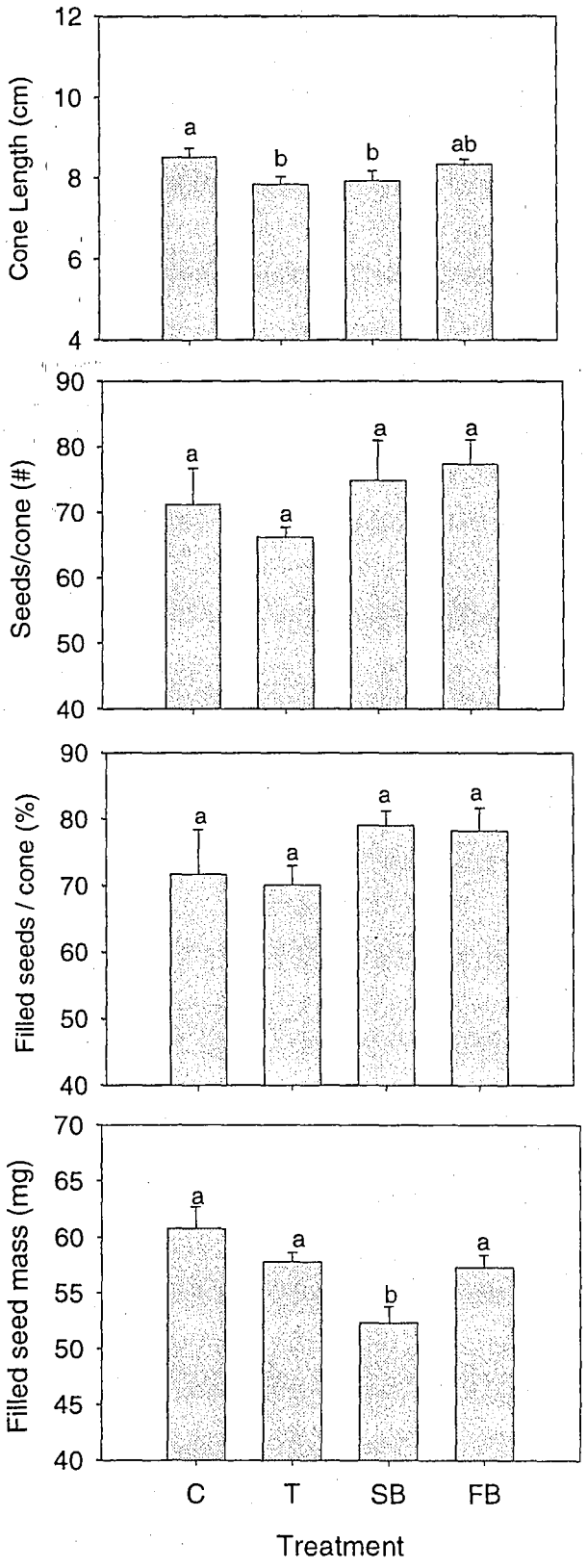
Cone Length (cm)
12
10
8
6
4
a
b
b
ab
Seeds/cone (#)
90
80
70
60
50
40
a
a
a
a
Filled seeds / cone (%)
90
80
70
60
50
40
a
a
a
a
Filled seed mass (mg)
70
65
60
55
50
45
40
a
a
b
a
C
T
SB
FB
Treatment

Figure 6

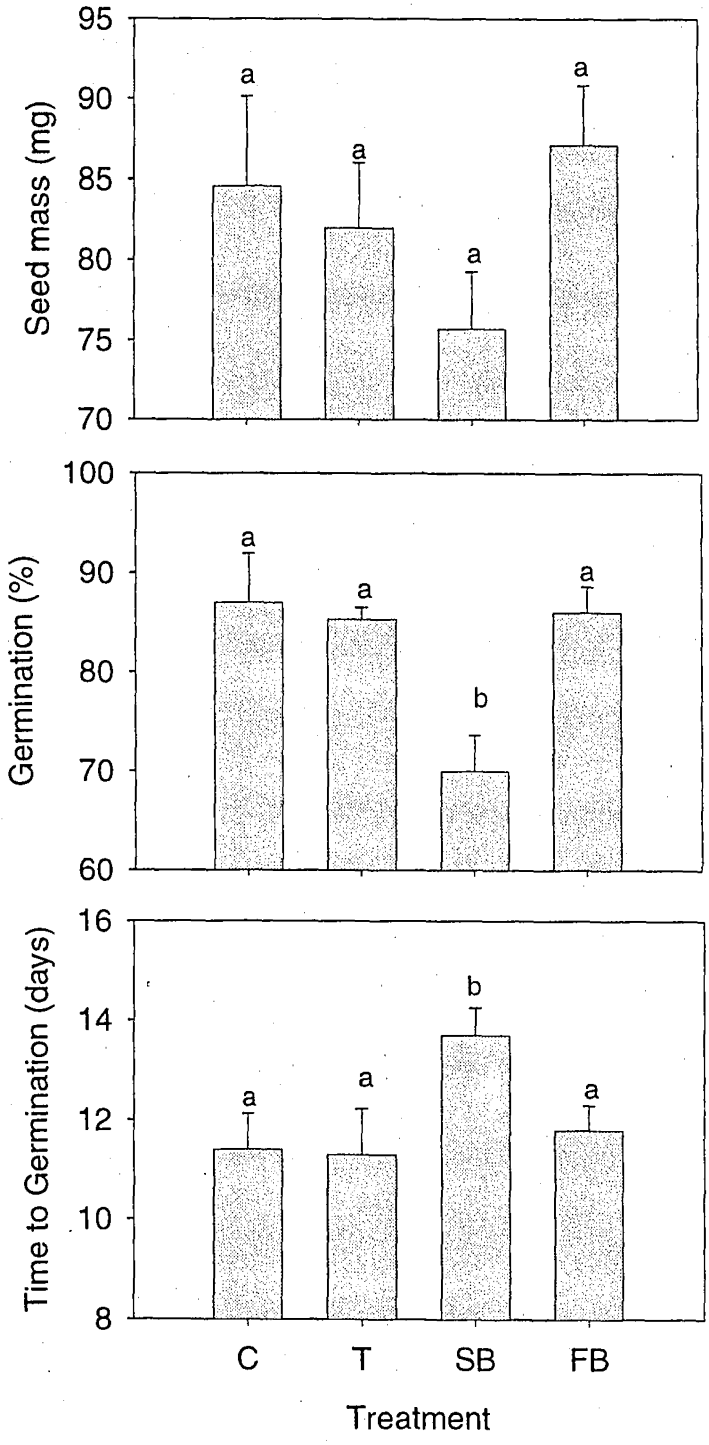
Seed mass (mg)
95
90
85
80
75
70
a
a
a
a
Germination (%)
100
90
80
70
60
a
a
b
a
Time to Germination (days)
16
14
12
10
8
a
a
b
a
C
T
SB
FB
Treatment

Figure 7

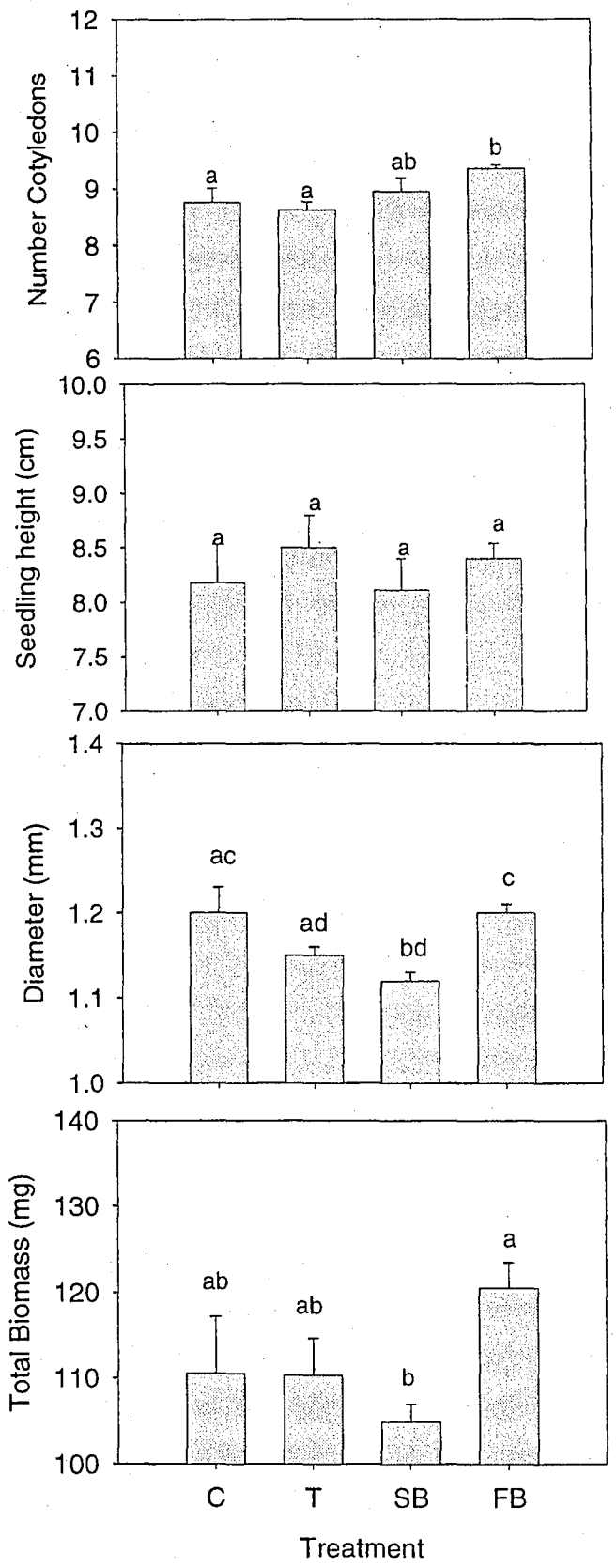
Number Cotyledons
12
11
10
9
8
7
6
a
a
ab
b
Seedling height (cm)
10.0
9.5
9.0
8.5
8.0
7.5
7.0
a
a
a
a
Diameter (mm)
1.4
1.3
1.2
1.1
1.0
ac
ad
bd
c
Total Biomass (mg)
140
130
120
110
100
ab
ab
b
a
C
T
SB
FB
Treatment

Figure 8